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BRYOLOGICAL PAPERS

I. THE ORIGIN OF AIR CHAMBERS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY, 100

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(WITH TWENTY-TWO FIGURES)

The air passages in certain tissues of the vascular plants are so prominent as to attract instant attention when a section is examined. Inasmuch as new cells are produced by division, and the partitioning wall is a joint product of the two severed protoplasts, a-priori reasoning leads to the hypothesis that intercellular spaces arise by the secondary splitting of the membrane, on account of unequal growth and turgor. This hypothesis is abundantly verified by observation, and there remains no doubt whatever that the aerating passages of vascular plants are formed in this manner.

When intercellular spaces were observed in liverworts, it was natural to assume that they took their origin in the same fashion. In the Anthocerotales, intercellular spaces of the triangular and quadrangular type, familiar in the pith parenchyma of vascular plants, occur in both gametophyte and sporophyte. We are not aware that the origin of these has ever been supposed to be in any way different from that of similar spaces elsewhere. The origin of the mucilage clefts and chambers of *Anthoceros* and *Dendroceros* is definitely ascribed by LEITGEB¹ to cleavage, and he has been quoted in all textbooks.

In the Marchantiales, however, the canals and air chambers in the upper portion of the thallus are so large and extraordinary in architecture, that it was questionable whether they arose in the familiar fashion, or had some peculiar origin. HOFMEISTER² describes the formation of the air chambers in the gametophore of *Marchantia polymorpha* in these words:

Close under the arched upper surface of the receptacle of *Marchantia* . . . numerous air cavities are formed, even before the first appearance of the arche-

¹ LEITGEB, H., Untersuchungen über die Lebermoose 5:4, 13ff., 31. 1879.

² Higher Cryptogamia 117. 1862.

gonia. They are formed in the same manner as the air cavities of the stem. At the first appearance of the air cavity one epidermal cell only detaches itself from the underlying tissue of the receptacle. By repeated transverse division of the mural rows of cells lying between the air cavities, the lid of the cavity is carried rapidly upwards. This epidermal cell, which closes the air cavity, forms itself into a stomate.

HOFMEISTER also speaks of air cavities being formed in the "stem" by the lifting-up of a "single layer of cells," of which the central one divides to form the ring that opens as a stoma.

This conception is obviously that of schizogenous formation, but the separation was ascribed to the upgrowth of the lateral walls of the chamber as the base and roof widen. With the exception of the detachment of a single epidermal cell, what HOFMEISTER describes actually happens; but he observed only the later stages of development and not the origin of the chambers.

This alleged origin was accepted by SACHS and was described by him in the *Lehrbuch der Botanik* of 1874, whence it found its way into the English edition, issued in 1882. There the statement occurs (under the topic *Intercellular spaces*, be it noted):

The epidermal cells become detached from those lying beneath over rhomboidal areas, which are marked off from one another by walls formed of cells which are not detached.

In the Appendix (p. 948), VINES, who had seen LEITGE's paper on the stomata of *Marchantia*,³ gives a very brief and clear outline of the formation of air chambers according to LEITGE. From that time to the present LEITGE's views have prevailed, being repeated in all the textbooks as settled fact. As CAMPBELL in the new edition of *Mosses and ferns* nowhere definitely describes the origin of air chambers,⁴ we quote and translate from GOEBEL's *Organographie* (p. 296):

It is characteristic of the Marchantiaceae and Ricciaceae that air chambers are found in the nutritive tissues. These arise, as LEITGE first showed, not at

³ Sitzb. Kais. Akad. Wiss. Wien 81:40-54. pl. 1. 1880.

⁴ CAMPBELL casually uses this expression (*op. cit.*, p. 39) regarding *Riccia trichocarpa*: "At first the cells of the young thallus are without *intercellular spaces*, but at an early period the outer cells of the young segments *separate* and form the beginnings of the characteristic air-spaces" [italics ours]. Inasmuch as CAMPBELL follows LEITGE's account for other Ricciaceae, so far as he gives any description of the air-chamber formation, these phrases seem to have been accidentally correct.

all as do the intercellular spaces of higher plants, by the cells separating, nor even by progressive cleavage from outside inward; but they appear originally as depressions in the surface, which arise by definite points (always situate where four cells meet) lagging in growth and so becoming overgrown by the adjacent parts.

While casually following the development of the spirelike air chambers on the gametophore of a species of *Fimbriaria* collected by Dr. C. J. CHAMBERLAIN in Mexico in 1904,⁵ our attention was attracted to very young air chambers on a receptacle still very small. The appearance of a cavity very close to the apical cell, and relatively deep in the tissue, raised a doubt as to the possibility of its having been overgrown so promptly by adjacent cells. On examining this matter in the thallus, in longitudinal sections through the apical cell, what we saw showed that a reinvestigation of the origin of the air chambers was needed.

Accordingly, we have examined as many of the Marchantiales as have been easily obtainable. Although we have not studied all the members of the group, but only representatives, the facts observed are so uniform and unambiguous that it is unlikely there is any other mode of origin than the one found in every case examined. This expectation derives force from the fact that our examination has covered all types of air chamber, and that LEITGE's extensive observations can be interpreted (as he himself confessed in regard to *Marchantia* and *Preissia*) in consonance with schizogenous origin.

Inasmuch as LEITGE's view is accepted at present and we consider it untenable, we quote some of his very unequivocal declarations, to show that he has left no doubt as to his meaning. Speaking of the Ricciaceae, after describing the quadratic surface mesh formed by the walls of the cells near the growing point, he says:⁶

Soon one observes at the corners small pits, which arise thus: the growth of the lateral walls of the outer cells, in so far as concerns the direction at right angles

⁵ Probably *Fimbriaria echinella* Gottsche.

⁶ Bald bemerkt man an den Ecken kleine Grübchen welche dadurch entstehen, dass das Wachstum der Seitenwände der Aussenzellen, insoweit als es sich in der auf der Dorsalfäche senkrechten Richtung vollzieht, in den Kanten geringer ist, als an den übrigen Stellen. Es entspricht daher der tiefste Punkt eines Grübchens dem (ursprünglich an der Oberfläche gelegenen) äussersten Punkte der verkürzt bleibenden Seitenkante, und die das Grübchen umgrenzenden Wandstücke sind Theile der ursprünglichen Aussenwände, resp. aus diesen hervorgegangen. Indem nun dieser

to the dorsal surface, is less at the corners than in the other parts. The lowest part of a pit therefore corresponds to the outermost point of the lateral wall, originally lying in the surface, which wall remains short, and the parts of the wall bounding the pit are parts of the originally outer walls, or have arisen from them. If this mode of growth be continued, the pit will of course be deepened. Now there occurs in each cell a division parallel to the surface, which separates approximately the part surrounding the pit from the inner part. From the exterior cell thus formed, there arises the whole of the tissue pervaded by air chambers. First of all, the pit becomes farther deepened into a canal by progressive growth in the same direction, and now there follows, in each outer cell, a division parallel to the earlier one. The canal now penetrates two layers of cells, of which the outer becomes the permanent epidermis, while from the inner arises the entire tissue containing the air chambers lying beneath the epidermis.

He continues:⁷

By way of summary of the foregoing exposition of the formation of air chambers and stomata, it may be said that *the air chambers do not arise in the tissue by the separation of cells, nor by a progressive splitting from outside inward*; but that they represent depressions of the surface, which are formed by definite points of the surface becoming overgrown by the more rapid growth of neighboring parts.

This investigation LEITGEB extended by a study of the stomata of Marchantiaceae, an account of which, published in 1880 (*l. c.*, footnote 3), was reprinted, with only a few unimportant verbal changes, in the last part of the *Untersuchungen*. After declaring the homology of the air chambers and canals of Marchantiaceae with those of

Wachstumvorgang noch weiter eingehalten wird, wird das Grübchen selbstverständlich vertieft. Nun erfolgt in jeder Zelle eine der Oberfläche parallele Theilung, welche ungefähr den die Grube umgrenzenden Theil derselben von dem inneren Theile abschneidet. Aus den so entstandenen Aussenzellen geht nun das ganze, mit Lufträumen durchzogene Gewebe hervor. Vorerst wird durch das in gleicher Richtung fortschreitende Wachstum das Grübchen weiter vertieft und so zum Canale, und nun erfolgt in jeder Aussenzelle eine der früheren parallele Theilung. Der Canal durchsetzt nun zwei Zelllagen, deren äussere zur bleibenden Oberhaut wird, während aus der inneren Zellschicht die ganze unter der Oberhaut liegende Lufthöhenschicht hervorgeht.—Untersuchungen über die Lebermoose 4:10. 1879.

⁷ In Zusammenfassung der über die Bildung der Lufträume und Spaltöffnungen eben gegebenen Ausführungen ergibt sich also, dass die Luftkammern nicht *im* Gewebe durch Auseinanderweichen der Zellen entstehen, auch nicht durch eine von aussen nach innen fortschreitende Spaltung; sondern dass sie Einsenkungen der Oberfläche darstellen, die dadurch gebildet werden, dass bestimmte Punkte der Oberfläche durch rascheres Wachstum benachbarter Partien überwachsen werden.—*l. c.*, p. 12.

Ricciaceae, and pointing out the existence of intermediate forms, he says:⁸

Further, there does not occur in the formation of the air chamber any separation of cells previously joined without interstices; nor does the roof of the air chamber (epidermis) lift itself up secondarily from the underlying tissues, but it is formed simultaneously with the rudiment of the air chamber and grows in breadth at equal pace with the broadening chamber.

Regarding *Preissia* he repeats:⁹

It (the formation of air chambers) begins with the formation of superficial pits, which deepen to canals that later become closed again outwardly, as in the carpophore.

And further:¹⁰

I have not discussed hitherto the origin of these primary pits. We *might* explain them by the splitting of the membrane, i. e., the separation of cells; and the formation of aerating apparatus with simple openings would then be con-

⁸ Es findet also bei Bildung der Luftkammer eine Trennung früher interstitienlos verbundener Zellen nicht statt, und die den Luftraum nach aussen abschliessende Decke (Oberhaut) hebt sich nicht secundär vom darunter liegenden Gewebe ab, sondern sie bildet sich schon zugleich mit der Anlage des Luftraumes, und wächst nach Massgabe seiner Verbreiterung ebenfalls in die Breite.—Unters. über die Lebermoose 6:6. 1881.

⁹ Sie beginnt mit der Bildung von oberflächlichen Grübchen, die sich zu einem Canale vertiefen, der später wie an den Fruchtköpfen nach aussen wieder verschlossen wird.—*l. c.*, p. 9.

¹⁰ Ich habe bis jetzt der Art der Entstehung jener primären Grübchen nicht Erwähnung gethan. Wir könnten sie durch Spaltung der Membran, d. h. durch Trennung der Zellen erklären, und es würde dann die Bildung des mit einfachen Oeffnungen versehenen Athmungsapparates als Folge einer von aussen nach innen fortschreitenden Membranspaltung zu betrachten sein, wo also die Bildung der Oeffnung der primäre, die der Athemhöhle (Luftkammer) der secundäre Vorgang wäre. Am Laube von *Marchantia* (und *Preissia*) würde aber zuerst die Athemhöhle, und zwar wieder durch Trennung der Zellen (Membranspaltung) erfolgen, und später erst würde der Athmungscanal—and wie die Beobachtung lehrt—von innen nach aussen fortschreitend gebildet werden. Für die Oeffnungen an den Fruchtköpfen müsste man selbstverständlich annehmen, dass hier ebenfalls die Spaltung von aussen nach innen fortschreite, dass die Spalte aber später durch Aneinanderschliessen der Zellen wieder verschwinde um erst weit später wieder geöffnet zu werden.

Ich glaube aber, dass eine andere Erklärung viel plausibler ist, weil sie geeignet ist, die Vorgänge von einem Gesichtspunkte aus zu betrachten, und sie mit anderen scheinbar ganz verschiedenen Bildungen in Uebereinstimmung zu bringen.

Ich habe im IV. Hefte meiner Lebermoosuntersuchungen die Ansicht aufgestellt, und zu begründen versucht, dass jene primären Grübchen nicht durch Membranspal-

sidered as a result of progressive cleavage of the membranes from outside inward, when the formation of the opening would be the primary, and that of the air chamber the secondary process. So on the frond of *Marchantia* (and *Preissia*) the air chamber would arise first (and indeed by cleavage of the cell walls), and only later would the aerating canal be formed (as in fact observation shows) progressively from inside outward. As to the openings on the carpophore, one of course would have to assume that here likewise the cleavage advances from outside inward, but that the cleft later disappears, on account of the pressing together of the cells, and only much later again becomes opened.

But I think that another explanation is much more plausible, because it is competent to consider the processes from a standpoint which brings them into harmony with other entirely different structures.

In part IV of my *Untersuchungen* I have set forth and sought to establish the view that each primary pit is not formed by cleavage of membranes, but arises in consequence of peripheral growth in thickness. The deepest point of the pit thus does not correspond with a point lying originally *within* the membrane of a lateral wall, i. e., below the surface, but lay originally in the outer surface, and the parts of the wall bounding the pit are therefore parts of the original outer walls, or have developed from them. If the same growth process (which is really only accelerated growth in area of the originally free outer walls) proceeds still further, the pit will be deepened. Now as the air chambers (to be) arise exclusively by growth in area of the parts of the walls bounding the pits, it follows that they must be regarded as really depressions of the surface, which are formed by certain

tung sich bilden, sondern in Folge des peripherischen Dickenwachstums entstehen. Der tiefste Punkt des Grübchens entspricht somit nicht einem ursprünglich innerhalb der Membran einer Seitenwand, also innerhalb der Oberfläche gelegenen Punkt, sondern war ursprünglich, in der Aussenfläche gelegen und die das Grübchen umgebenden Wandstücke sind daher Theile der ursprünglichen Aussenwände, respective aus ihnen hervorgegangen. Indem der gleiche Wachsthumsvorgang (der eigentlich ja nur ein gesteigertes Flächenwachsthum der ursprünglichen freien Aussenwände ist) noch weiter eingehalten wird, wird das Grübchen vertieft. Da nun die späteren Luftkammern ausschliesslich durch Flächenwachsthum der die Grübchen begrenzenden Wandstücke entstehen, so folgt daraus, dass sie eigentlich als Einsenkungen der Oberfläche zu betrachten sind, die dadurch gebildet werden, dass bestimmte Punkte der Oberfläche durch rascheres Wachsthum benachbarter Partien überwachsen werden. Es trifft hier bestimmte Punkte der Oberfläche ganz dasselbe Schicksal, wie die anfangs sogar über die Oberfläche hervorragenden Mutterzellen der Geschlechtsorgane, welche ja ebenfalls durch Ueberwachsen ins Gewebe versenkt werden. Die Höhlungen, in welchen die Antheridien und Archegonien z. B. bei *Riccia* liegen, entsprechen in ihrer Bildung vollkommen den Luftkammern, und da beide gleichzeitig angelegt werden, müssen sie auch in gleiche Tiefe in das Gewebe hineinreichen, mit andern Worten, die Basis der Geschlechtsorgane liegt in gleichem Tiefe mit der innern Begrenzung der Lufträume, und wo die Organe zu Ständen zusammentreten, sind diese ihrer ganzen Tiefe nach von Luftkammern durchzogen und sitzen unmittelbar dem interstitiellen Gewebe auf.—*l. c.*, p. 9.

points of the surface becoming overgrown by reason of the more rapid growth of neighboring parts. There befalls these points quite the same fate as overtakes the mother cells of the sex-organs, which at first indeed project above the surface, but likewise become sunk in the tissue by being overgrown. The hollows in which lie the antheridia and archegonia (e. g., of *Riccia*) correspond completely in their formation with the air chambers; and as both are laid down simultaneously, they must attain an equal depth in the tissues; in other words the base of the sex-organs lies at the same level as the inner boundary of the air chambers; and where the sex-organs are aggregated in groups, they are surrounded for their whole length by air chambers and are seated directly upon the compact tissue.

There is no doubt as to LEITGEB'S meaning, for he has both put his declaration positively and denied categorically the other possible modes of origin. Yet it is clear, both from his figures and from his description, that he saw many clefts which can be most easily interpreted as due to splitting; but apparently he did not in all cases see the earliest stages of the air chambers, which can be interpreted in no other way. It is not surprising, however, that so good an observer missed them, as he had at his command almost none of the modern technique. Rather it is surprising that he saw so much and so accurately, for with the best technique it is not easy to discern the first cleavage.

A-priori reasoning, weak as it is, creates suspicion of the correctness of LEITGEB'S view, and no figure of his shows any condition that cannot be interpreted in consonance with schizogenous origin. It is peculiarly difficult to conceive of a mode of growth such as he describes, for nothing like it is known elsewhere. If the lowest point of the pit is a point which originally lay in the surface, and there is no cleavage, then the progressive formation of the pit must be somewhat as in *fig. 1*. In such a process the pit must be very slender, as otherwise the wall would show a reentrant angle; indeed, it is difficult to see why the pit would not be closed by turgor as fast as the adjacent cells grew up, unless one predicates rigidity at the base of the dome or a rapid growth at the very surface in which the upgrowing cells did not share. When ready for the divisions which are to pro-

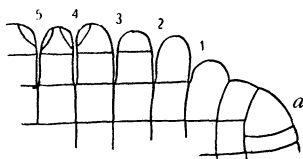


FIG. 1. — Diagram of the origin of air chambers according to LEITGEB.

vide a roof for the widening chamber, the form of the cell, necessary under this mode of growth, would seem almost to preclude so unequal a division (4, *fig. 1*). Certainly if the pit were open at the time the first division took place, the cells cut off could only close it by later growth. As a matter of fact, in LEITGEB's plates no such stages as we have sketched are shown; yet if the pit is formed as he says, they should be found. In spite of diligent search we have seen nothing that could possibly be interpreted so.

Moreover, it is easy to see that LEITGEB was misled by his desire to homologize the formation of air chambers with the formation of pits for the sex-organs. So, though he admits seeing the primary formation of intercellular spaces in *Marchantia*, *Preissia*, and *Plagioclasma*, he deliberately rejects the obvious explanation of splitting. He did this in order to apply to *Marchantiaceae* the idea he had conceived for *Ricciaceae*. So if it can be shown in *Ricciaceae* that the intercellular space is formed by cleavage, and then splits out to the surface, the immediate reason for such distortion will have been cleared away, though it cannot be justified. Having homologized the air chamber and sex-organ pit in *Ricciaceae*, he applied the explanation perforce to *Marchantiaceae*.

Now in the case of sex-organs, it is easy to understand how the rudiment can be overgrown and left in a pit, since the growth of a whole cell line is retarded, while its neighbors surpass it. The initial at first grows more rapidly than do the adjacent cells of the thallus, the protuberance and finally the protrusion of the initial being the visible evidence of its more rapid growth. Later the adjacent cells outgrow the sex-organ and it becomes "sunk" in the thallus.

But in the matter of air chambers is involved the retardation or the cessation of growth in a very limited part of the walls belonging to four contiguous cells, while all the rest of these four walls and the remaining sixteen grow throughout, and all decidedly outgrow the lagging portion of the four! While such a thing is not impossible, it is wholly improbable and needs to be supported by most convincing evidence. Such evidence LEITGEB nowhere presents, either in text or figure. We propose to show, on the contrary, that the assumption of such peculiar lagging is unnecessary, because all the observed structures can be produced by common splitting, and the earlier stages

can be produced in no other way. In presenting the evidence we have selected only a few examples, and show in the drawings merely the walls, since to show the cell contents would only obscure the essential features.

In the Ricciaceae we have examined only *Riccia fluitans* and *R. natans*, in which the origin of the air chambers is exactly alike, though the later course of development seems to be different. The origin of both is certainly by internal cleavage, and it is quite evident that the air chamber is wholly unrelated to the sex-organ pit. *Fig. 2* furnishes conclusive evidence on both points. An apical cell (?) is at *a*; at ¹ is a young cleft and at ² an older one, which has promptly broken out to the surface; while ♀ is a young archegonium. The fact that this organ is not yet

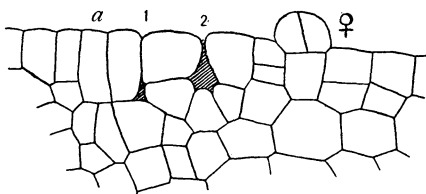


FIG. 2.—*Riccia natans*: *a*, apical cell (?); ¹, ², air chambers; ♀ young archegonium.

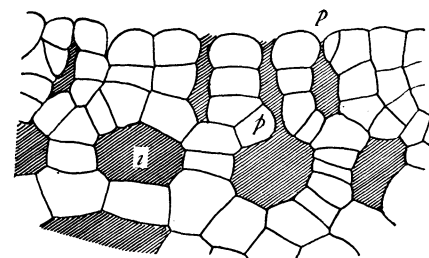


FIG. 3.—*Riccia natans*. Older air chambers; *i*, internal; at *p*, *p*, partial closure of passage by outgrowing cell.

overgrown by the adjacent tissues, while the air chamber ² is clearly defined, shows forcibly how LEITGEB erred in homologizing the sex-organ pit and the air chamber. In *figs. 3, 4*, further stages of development are shown and also the tendency of the spaces to close at certain points, *p*, both at surface and internally by the outgrowth of cells.

The peculiar form of the thallus and the sudden tumefaction of the tissues in *Riccia natans* makes it very difficult to trace the history in detail, and we are not prepared to make any statement at present as to the later course of development of the air chambers. The system appears to be a complicated one; there is rapid enlargement of primary spaces, probably accompanied by secondary cleavage and partitioning of the chambers.

In *Marchantia* the splitting does not take place so early in the

history of any segment and the enlargement of the intercellular spaces proceeds much more slowly. Moreover, the structure of the thallus

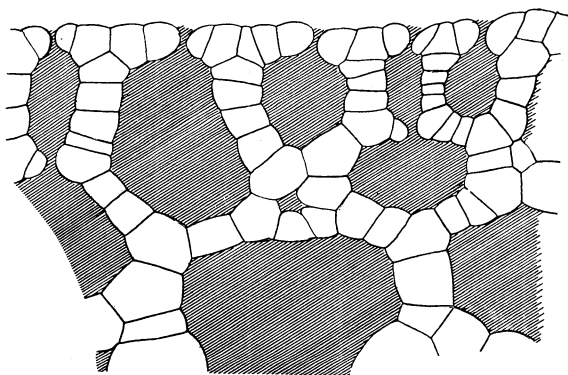


FIG. 4.—*Riccia natans*. Nearly mature air chambers, superficial and internal, primary and secondary.

makes it easier to secure sections through the apical region, so that one may readily observe the origin and follow the development of the air chamber. It seems probable from our observations that the time and place of the first splitting is

somewhat variable, depending upon the relation between cell division and enlargement.

The normal position of the cleft is either in the center of a segment of the apical cell near the surface or in the center of one or another of its primary surface segments

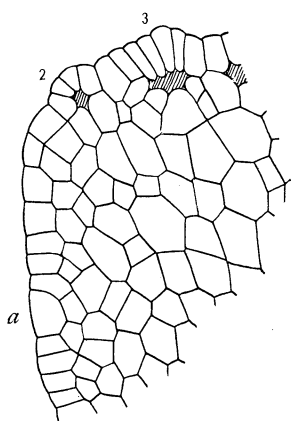


FIG. 6.—*Marchantia polymorpha*: a, apical cell; 2, 3, air chambers.

surface segments formed by a further division. A periclinal division of the segment may cut it into a superficial and an internal cell. This superficial cell is oftenest the mother cell of the chamber (fig. 9). Then

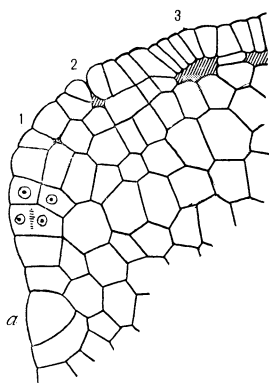


FIG. 5.—*Marchantia polymorpha*: a, apical cell; 1, 2, 3, air chambers.

two anticlinal walls, ² 2, and another, ³, in the plane of the drawing, divide this "mother cell" into four, a dextral and sinistral, an anterior and

a posterior cell. Each is then divided, in the plane ^{4 4}, into a superficial and an internal cell by a periclinal division, and at the intersection of these last walls with the preceding anticlinal one, ^{2 2}, the split usually occurs. This is promptly followed by divisions, ^{5 5}, to form the cells of pore margin and roof. In *fig. 5* the four nuclei mark the place of the split; for were the division in progress completed, the cleft would appear at the corner common to these four cells.

There is also more or less variation in the course of development. Sometimes the nascent chamber breaks out to the surface and remains wide open for a time (*fig. 7, 2*); sometimes (and more commonly) divisions

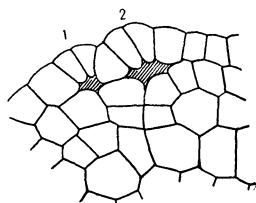


FIG. 8.—*Marchantia polymorpha*: 1, 2, air chambers; 2 shows tardy division of roof cells.

ensue so promptly in the cells above the primary cleft that the turgor of the newly formed cells keeps the passage closed from the beginning (*figs. 6, 3; 8, 1, 2*). These quickly divide (*figs. 6, 3; 7, 3; 9*) and by repeated divisions give rise to the roof and the pore margin (*fig. 10*) of the well-known form.

A comparison of these figures with *fig. 17, plate 12*, of LEITGEB'S *Untersuchungen*, and the earlier figures of his paper on the stomata of *Marchantia* (*l. c.*, footnote 3), shows clearly enough that he saw essentially similar stages, though probably not such early ones as we indicate. It was chiefly in the interpretation of his observations that he went astray.

In *Lunularia* the process is similar in all respects to that in *Marchantia*, though the material available was

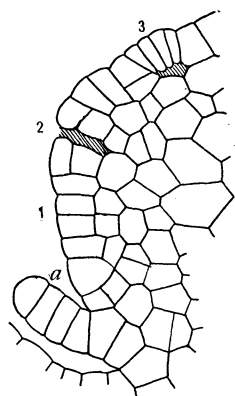


FIG. 7.—*Marchantia polymorpha*: a, apical cell; 2, 3, air chambers; at 1 the next one is due after division of outer cells.

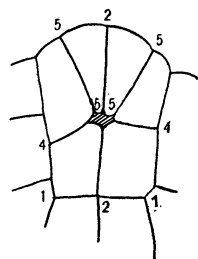


FIG. 9.—*Marchantia polymorpha*. Diagram of the course of normal division of the "mother cell" of an air chamber; the numbers show the sequence of walls.

not as vigorous as could have been desired. The splitting is prompt and the divisions follow so quickly that the roof and cells of the pore margin are soon completed (fig. 11).

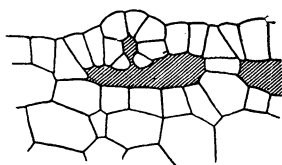


FIG. 10.—*Marchantia polymorpha*. Formation of the pore margin, with complete closure.

In *Conocephalus* also the formation of the air chamber is rapid (figs. 12, 13) and the details are not as regular and therefore not as easy to follow as the *Marchantia*. After the initial cleft has extended to the surface (fig. 12, 2) the expansion of the tissues at first outstrips the divisions which are to produce the roof, so that the chamber is open (fig. 12, 3, 4, fig. 13, 3, 4). Later the roof closes the chamber, perhaps intermittently (fig. 12, 5, fig. 13, 4, 6), which only becomes

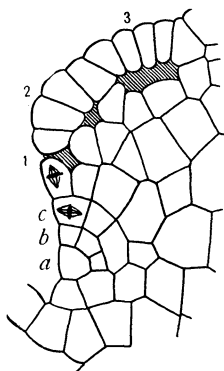


FIG. 11.—*Lunularia vulgaris*: *a*, apical cell; *b*, *c*, successive segments; 1, 2, 3, air chambers.

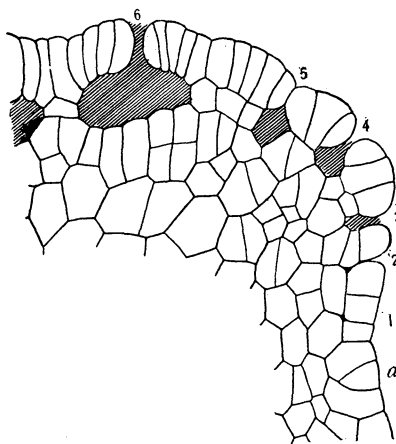


FIG. 12.—*Conocephalus conicus*: *a*, apical cell; 1-6, air chambers.

permanently open when the divisions for the pore margin begin (fig. 13, 6, 7).

Dumortiera (figs. 14, 15) forms air chambers that later disappear more or less completely, leaving only traces of their rhomboidal outlines on the surface.¹¹ The plants grow in very damp places, and all

¹¹ CAMPBELL found no evidence of air chambers in *D. trichocephala*, which we have not seen. It would be very remarkable if the early stages were wholly wanting.

the tissues concerned with the formation of air chambers have an oedematous look, being soon greatly swollen, with scanty contents.

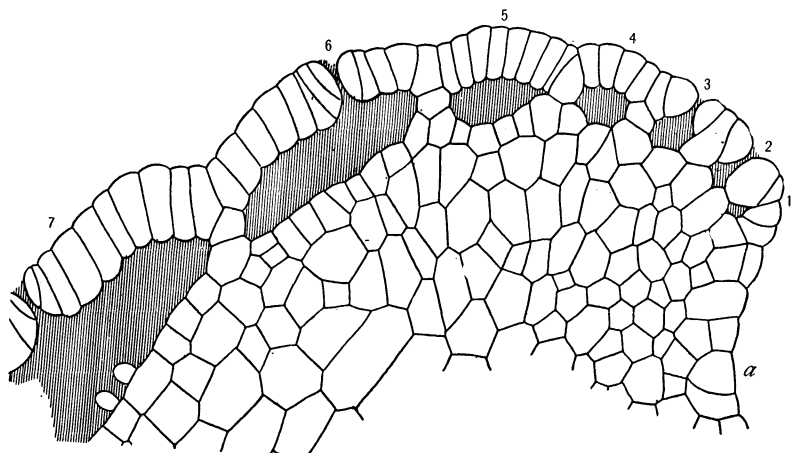


FIG. 13.—*Conocephalus conicus*: *a*, apical cell; 1-7, air chambers.

In consequence of the excessive turgor, apparently, the splitting is very prompt and complete, so that the young internal space is difficult to find. The air chambers develop rapidly, and “blow up,” so to speak, within a short distance of the apex, only the ragged walls and roofs, in section like a letter Y, remaining for a time.

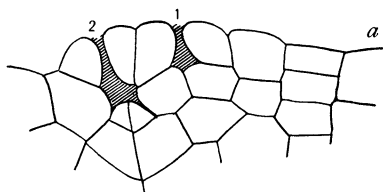


FIG. 14.—*Dumortiera hispida* (?): *a*, apical region; 1, 2, air chambers.

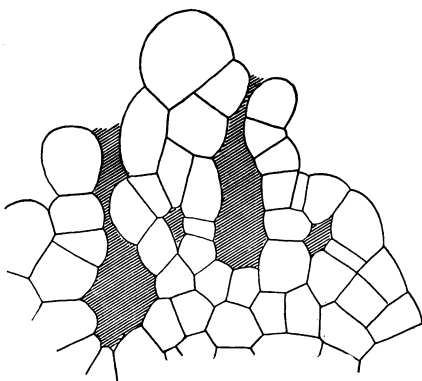


FIG. 15.—*Dumortiera hispida*. Older air chambers, deformed by excessive turgor.

It will be observed that the air-chamber region in *Marchantia*, *Lunularia*, *Conocephalus*, and *Dumortiera* is superficial. By no

means all of the tissues arising from the dorsal segments of the apical cell show splitting, but much the greater part is compact, with no inter-

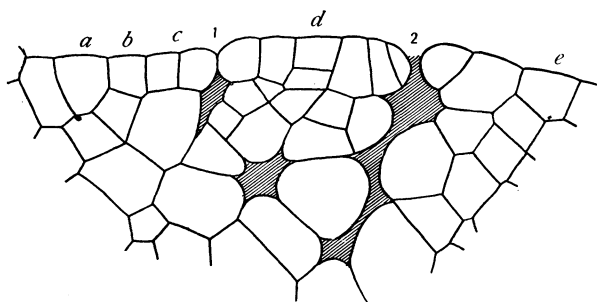


FIG. 16.—*Fimbriaria echinella*: *a*, apical cell; *b*–*e*, successive segments; 1, 2, air chambers; in *d* a secondary deep-seated cleft.

cellular spaces of any kind. In *Fimbriaria* and *Plagiochasma*, however, the splitting involves all the tissue which arises from the dorsal segments of the apical cell, so that a much greater part of

the thallus is permeated by extensive and irregular air passages (fig. 16), which make it almost as spongy as *Ricciocarpus*.

In *Fimbriaria* the primary splitting usually begins between the cells arising from successive segments (fig. 16, 1, 2, where 1 lies between segments *c* and *d*, and 2 between *d* and *e*). Later, and often deep in the tissue, secondary splitting gives rise to intercellular spaces which may reach the surface or may break into a primary space.

In *Plagiochasma* the splitting is likewise more pronounced between the offspring of different segments (fig. 17), but the secondary splitting, if such it may be called, occurs so promptly and becomes so extensive as to be hardly distinguishable from the primary (figs. 18, 19, 3a, 4a). The air passages are open almost or quite uninterruptedly until

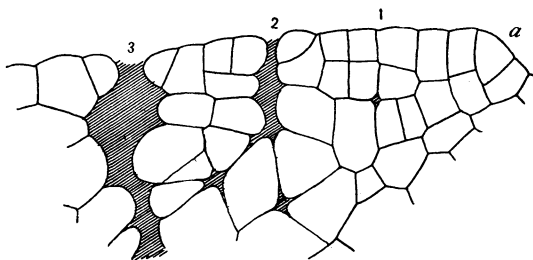


FIG. 17.—*Plagiochasma* sp: *a*, apical cell; 1–3, air chambers.

the pore margin is well begun (fig. 20). There is never a wide and shallow chamber, over whose increasing area a roof forms, *pari passu*;

but the passages are always deep and narrow, with hardly more than the pore margin for a roof (*fig. 21*). There are many spaces near the

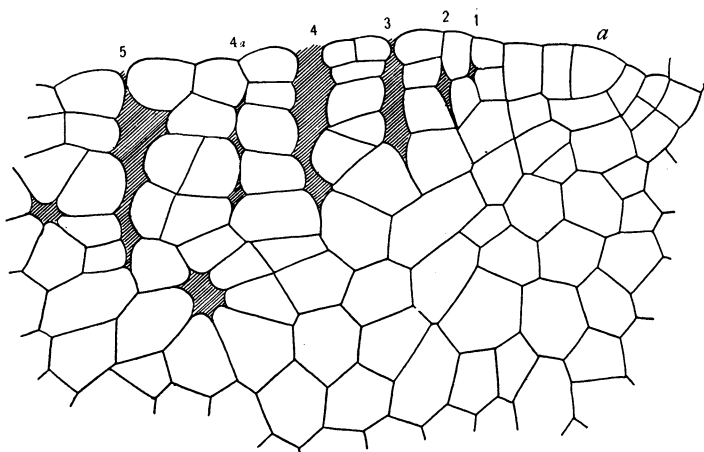


FIG. 18.—*Plagiochasma* sp.: *a*, apical cell; 1-5, air chambers; 4a secondary splitting between primary clefts 4, 5.

surface which have no direct opening by pore (*fig. 22, c*). These connect doubtless with the spaces that do have pores (*fig. 22, o*). Whether partitioning of the chambers occurs, as described by LEITGEB,

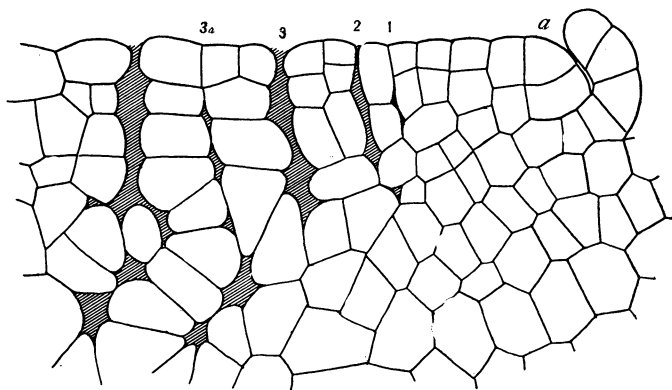


FIG. 19.—*Plagiochasma* sp.: *a*, apical cell; 1-4, air chambers; 3a, secondary splitting.

by the outgrowth of cell plates in *Plagiochasma* and in *Ricciocarpus*, we have not fully determined, though it appears probable; but the

formation of the aerating system is mainly due to splitting and growth.

How LEITGEB discounted the evidence of his eyes is well shown in the case of *Plagiochasma*, in which he saw and figured intercellular spaces,¹² as to which he remarks:¹³

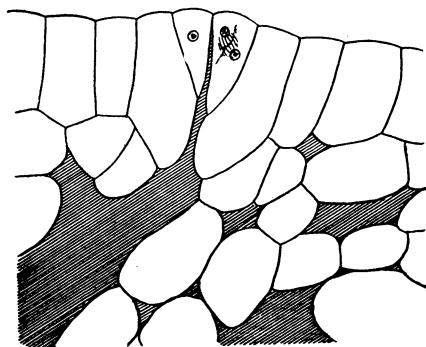


FIG. 20.—*Plagiochasma* sp. Beginning of pore margin.

In *P. Aitonia* they (the air chambers) appear in both longitudinal and cross-sections very commonly in the form of extremely small intercellular spaces, like those in ordinary parenchyma, and one could scarcely dismiss the idea that they are formed by cleavage in originally compact tissue, did not corresponding relations in other species speak against this interpretation.

As a matter of fact, corresponding relations in other species do not speak against this interpretation, but confirm it.

Finally we may point out that, instead of homologizing the formation of the air chambers in Marchantiales with the formation of sex-organ pits, which it required considerable distortion of the facts to do, we have brought their origin into line with the much more

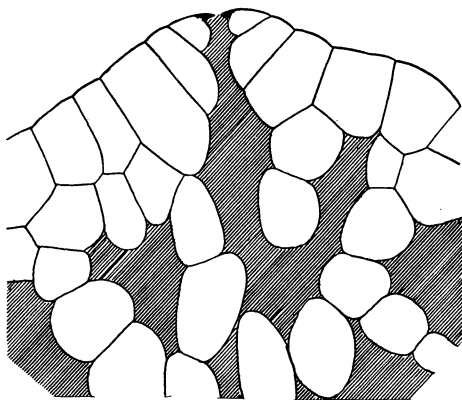


FIG. 21.—*Plagiochasma* sp. Pore margin complete.

¹² Untersuchungen über der Lebermoose 6: pl. I. fig. 4.

¹³ Bei *Pl. Aitonia* erscheinen dieselben an Längs- wie Querschnitten sehr häufig in Form äusserst kleiner Interzellularräume, wie sie im gewöhnlichen Parenchym vorkommen und man könnte die Annahme, sie entstanden durch Spaltungen in ursprünglich fest gefügtem Gewebe, kaum von der Hand weisen, wenn nicht die entsprechenden Verhältnisse bei den übrigen Arten gegen diese Deutung sprechen würden.—l. c., p. 64.

general phenomenon, the formation of schizogenous intercellular spaces.

Our conclusions may be summarily stated thus: The air chambers of Marchantiales arise invariably by the splitting of internal cell walls, usually at the junction of the outermost and first internal

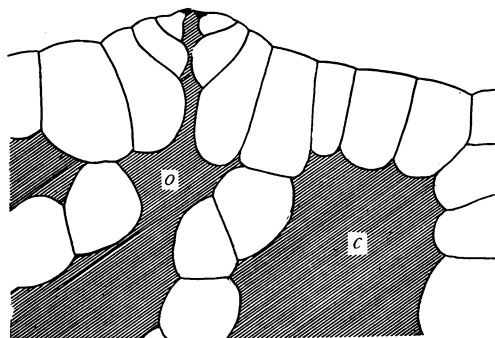


FIG. 22.—*Plagiochasma* sp.: *o*, air chamber opening through pore; *c*, closed chamber.

layer of cells. Thence, in one type splitting proceeds outwardly and inwardly more extensively than laterally, and lateral enlargement of the chamber follows by growth; while in the other type expansion of the chamber is due to extensive inward splitting accompanied by growth. The origin of the air chamber is in all respects like that of intercellular spaces in the vascular plants.

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NOTE.—The figures are all drawn to the same scale and appear here magnified about 550 diameters.